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Revisiting the non-native insect fauna of Greece: Current trends and an updated checklist

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Abstract

Alien invasive species not only have adverse environmental impacts, they may also pose socioeconomic and human health threats. The increase in detected non-native (alien) and cryptogenic species, followed by the necessity for up-to-date scientific information on biological invasions, prompted a thorough literature investigation on the non-native entomofauna of Greece. Supplementing previous studies concerning Europe and Greece, a checklist for the non-native insect species of the country is provided, while their number is elevated from 266 to 469. Current trends regarding species richness and taxonomy, deliberate or accidental means of introduction, as well as their native range and trophic preferences are analysed and discussed. This publication illustrates the current state of non-native insects of Greece, highlighting the need for an effective early warning system integrated in national phytosanitary legislation, survey protocols and strategies towards the eradication and mitigation of their detrimental impacts.

Keywords

Checklist, insects, invasive species, non-native, trends

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Introduction

Human-mediated species translocations, mostly due to globalisation and international trade, have gradually led to an unprecedented rise in the number of non-native species across the world and which is showing no signs of saturation (Hulme 2009; Seebens et al. 2017). These extraordinary species movements have been indicated as the major cause of a breakdown of "classical" biogeographic regions, through the previously impossible overcoming of geographic dispersal barriers (Capinha et al. 2015). As a consequence, in an era of continuous biotic homogenisation, climate and socioeconomic relationships are foreseen to define biogeography and species assemblages worldwide (McKinney and Lockwood 1999; Capinha et al. 2015).

Invasive alien species (IAS) are responsible for the global loss of biodiversity through, for example, competition with and replacement of native species, pathogen transmission, alteration of food webs and the reduction of habitat complexity (Simberloff et al. 2013; Chinchio et al. 2020). By extension, IAS not only hamper species richness, turnover and distribution, but also they inhibit ecosystem services (Vilà and Hulme 2016). Regarding the socio-economic impact, IAS have been estimated to cost the EU around 12 billion euros annually at least (Kettunen et al. 2009). Additionally, beside the phytosanitary risk, various alien species have been deemed as a public health hazard through the transmission of diseases and allergens, the infliction of venomous bites or the release of poisonous toxins (Schindler et al. 2015; Peyton et al. 2020). These pervasive, contemporary challenges reinforce the necessity for further research on and constant update of the non-native species regarding their introduction, establishment and distribution, but also mitigation of their adverse impact and possible eradication.

The first comprehensive checklist of alien species for Europe was delivered by the DAISIE project (Delivering Alien Invasive Species Inventories for Europe; DAISIE 2009). Under this project, a total of 1306 non-native insects were catalogued (Roques et al. 2009). Since then, the total number of introduced insects in Europe has increased and, according to the available data from the European Alien Species Information Network (EASIN), currently approaches 3000 (of which ca. 1120 are alien within Europe), accounting for approximately one fifth of the total number of alien species in the continent (EASIN 2021).

In Greece, the first national checklist of non-native insect species was published by Avtzis et al. (2017), identifying 266 species. Pursuing the need for up-to-date scientific information on alien species (Tsiamis et al. 2016), this study aims to integrate recent, as well as previously neglected data on the non-native insect species of the country. In this publication, the previously published national checklist (Avtzis et al. 2017) is thoroughly revised, elevating the number of non-native insect species to 469. In addition to complementing the checklist, we discuss the current trends and invasion patterns regarding taxonomy and species richness, status, means of introduction, origin and trophic preferences. The provided checklist and interpreted data are intended to act as a first step towards establishing effective national phytosanitary legislation, a protocol for surveys and a national strategy towards the eradication and mitigation of impacts of non-native insects.

Materials and methods

A thorough literature survey supplementing the previous checklist of non-native insects (Avtzis et al. 2017) led to a large number of peer-reviewed journal articles concerning biological invasions of insects in Greece. Moreover, museum collection data (e.g. Caspers and Creuwels 2020; Fägerström 2020) and records on online databases (e.g. Bahr et al. 2017; Noyes 2019) were integrated into the catalogue. The previous study of Avtzis et al. (2017) focused only on DAISIE records of non-native insects, published until the end of 2014. In this study, additional records, published from January 2015 to 20 January 2021 (e.g. Davranoglou and Koutsoukos 2018; Leivadara et al. 2018; Kalaentzis et al. 2019; Demetriou et al. 2020; Kazilas et al. 2020), as well as previously overlooked publications (e.g. Mroczkowski 1965; Eliopoulos et al. 2002; Koveos et al. 2002; Gatt 2007; Martinou et al. 2011), are also included.

Following the methodological approach of Avtzis et al. (2017), species that have been recorded prior to the 16th century were excluded. Additionally, native or migrating species that were included in the previous checklist (Avtzis et al. 2017), were excluded from the present study. Synonymised taxa and biological control agents which failed to be established or with questionable presence were also removed from the checklist, namely: *Rhyzopertha dominica* (Fabricius, 1792) (Panagiotakopulu and Buckland 1991); *Tribolium confusum* (Jacquelin du Val, 1868) (King 2010); *Lasius turcicus* (Santschi, 1921) (Georgiadis, pers. comm.); *Pheidole megacephala* (Fabricius, 1793) and *P. teneriffana* (Forel, 1893) (Salata et al. 2019); *Aphidius colemani* Viereck, 1912, *Dirhinus giffardii* Silvestri, 1913 and *Aphytis lingnanensis* Compere, 1955 (Gerber and Schaffner 2016); *Danaus chrysippus* (Linnaeus, 1758) (Pamperis 2009).

Data on species taxonomy, status, origin, regime and means of introduction (intentional or unintentional) were pooled (Rabitsch 2010; Roques 2010) and statistically analysed in R STUDIO Version 1.2.5042 (R Studio Team 2021). The status of non-native species was catalogued as either alien or cryptogenic, the latter being attributed to species of unknown origin, which are neither demonstrably native nor introduced (Carlton 1996). Origin was interpreted according to biogeographic realms (Udvardy 1975; Snow et al. 1998) and not continents as opposed to Avtzis et al. (2017). Species originating from tropical/subtropical regions were not assigned to certain biogeographic realms due to the vast geographic range that the region covers. Instead, the category was included verbatim as given in Coeur d'Acier et al. (2010), Denux and Zagatti (2010), Pellizzari and Germain (2010), Reynaud (2010) and Sauvard et al. (2010). Species native to multiple biogeographic realms were catalogued accordingly. In agreement with the previous study, Regime consists of four different trophic guilds, namely phytophagous, detritivorous, parasitic and predator species (grouped), while species with unknown trophic preferences were treated as such.

Results

Taxonomy and species richness

The complete list of established non-native insect species of Greece is provided (Suppl. material 1). A total of 469 species from 13 orders and 117 families were catalogued (Table 1). Beetles (Coleoptera) are recorded as the richest order accounting for 30.5% of non-native insect species, followed by Hemiptera holding 29.6%. Hymenoptera follow, containing almost one fifth of species (19.4%) while butterflies and moths (Lepidoptera) and flies and allies (Diptera) combined, contain about one tenth of the total number of species (5.8% and 5.1%, respectively).

Compared to the previously recorded 266 non-native species (Avtzis et al. 2017), the current total number is increased by 76%. However, if we take into account the nine aforementioned species that were excluded, new additions increase the total number of non-native insects from the previous checklist by 82% that is, by 212 species. The change in order representation of this study compared to the previous checklist is shown in Fig. 1.

Origin – status

The origin of alien insects in Greece (excluding cryptogenic species), is summarised in Fig. 2 and Table 2. The Indomalayan, Nearctic and Eastern Palearctic biogeographic realms account each for about one fifth of alien insect species (21%, 21% and 20%, respectively). The Afrotropics contribute 14% of the total species number, followed by the Neotropics responsible for 10%. Only 6% of the country's alien entomofauna originate back to the remote Australian realm, while the lowest percentages were recorded from Western Palearctic and Tropical/Subtropical Regions (4%).

Of all species recorded in this report, 76% account for species alien to Greece, while cryptogenic taxa represent the remaining 24% (112 species) (Table 3).

Table 1. Family and species richness of the non-native insect species of Greece.

Order	Families	Species	% Species
Blattodea	2	3	0.6
Coleoptera	28	143	30.5
Dermaptera	2	2	0.4
Diptera	12	24	5.1
Hemiptera	24	139	29.6
Hymenoptera	19	91	19.4
Lepidoptera	13	27	5.8
Mantodea	1	2	0.4
Phthiraptera	5	7	1.5
Psocoptera	6	14	3.0
Siphonaptera	2	3	0.6
Thysanoptera	2	13	2.8
Zygentoma	1	1	0.2
Total	117	469	

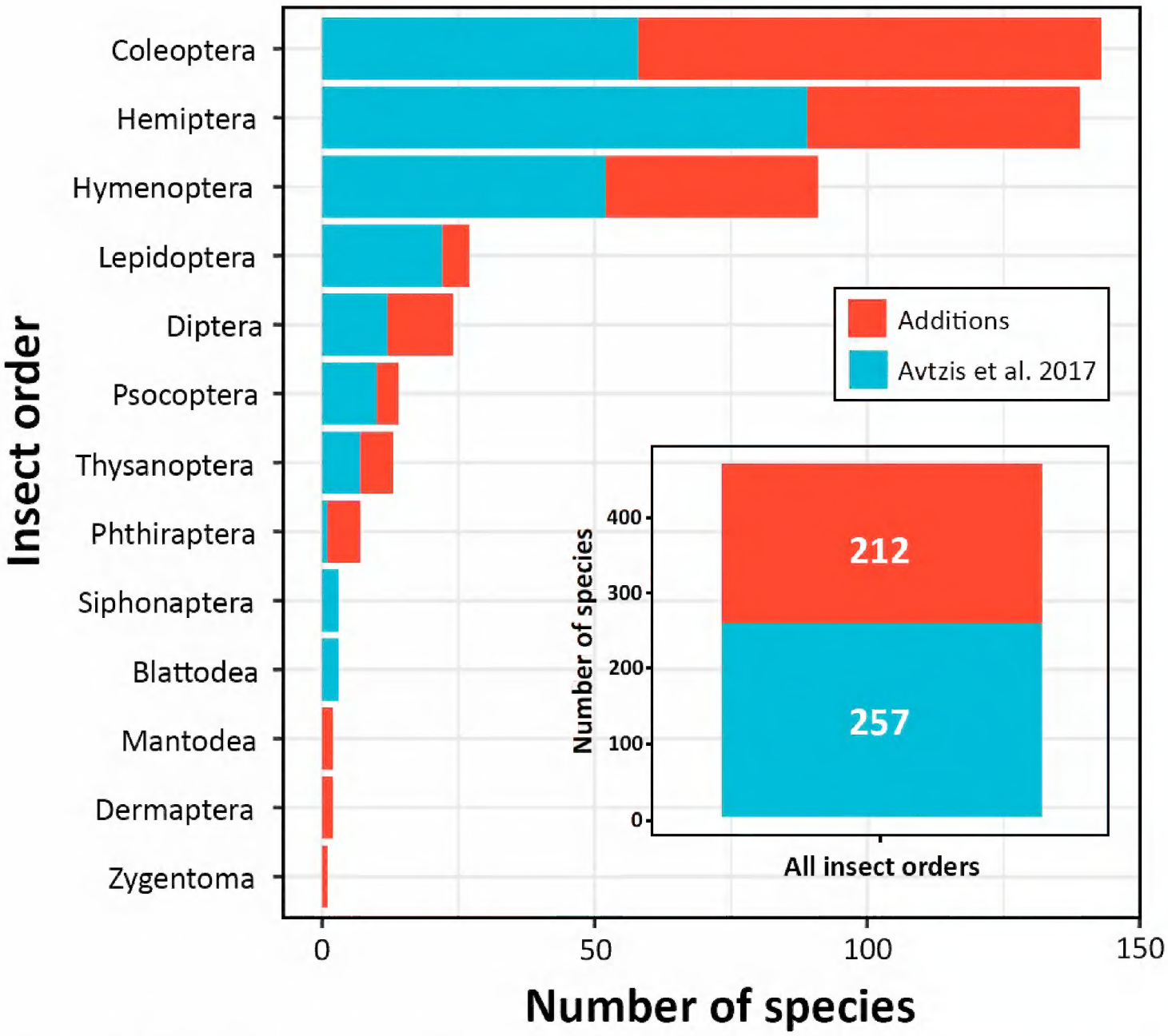

Figure 1. Number of non-native insect species per order. The number of species as in Avtzis et al. (2017) is coloured blue, while additions from this study are coloured red.

Table 2. Origin of non-native insect orders of Greece, excluding cryptogenic species.

Order	Origin							
	Western Palearctic	Eastern Palearctic	Afrotropical	Indomalayan	Australian	Nearctic	Neotropical	Tropical/ Subtropical
Blattodea	0	0	2	0	0	0	0	0
Coleoptera	6	16	15	26	9	13	14	10
Dermaptera	0	1	0	1	0	0	0	0
Diptera	0	0	3	2	1	8	2	0
Hemiptera	6	31	9	23	6	33	13	5
Hymenoptera	2	20	20	20	7	23	6	0
Lepidoptera	1	5	3	6	2	2	3	0
Mantodea	1	1	1	0	0	0	0	0
Phthiraptera	0	0	0	0	0	1	0	0
Psocoptera	1	2	0	2	0	1	0	0
Siphonaptera	0	1	1	0	0	0	0	0
Thysanoptera	0	1	2	3	1	2	3	1
Zygentoma	0	0	0	0	0	0	0	0
Total	17	78	56	83	26	83	41	16

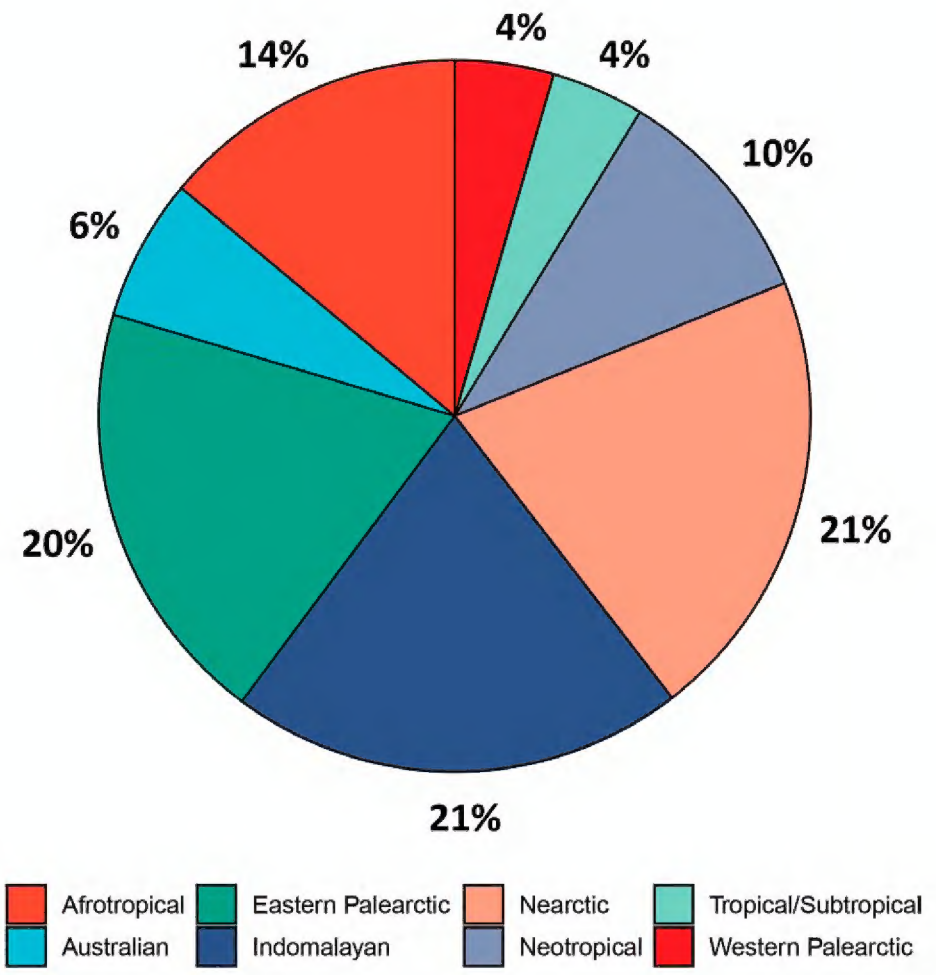

Figure 2. Origin of insect species alien to Greece.

Table 3. Status of non-native insect orders of Greece.

Order	Status	
	Alien	Cryptogenic
Blattodea	2	1
Coleoptera	98	45
Dermaptera	1	1
Diptera	16	8
Hemiptera	119	20
Hymenoptera	82	9
Lepidoptera	18	9
Mantodea	2	0
Phthiraptera	1	6
Psocoptera	4	10
Siphonaptera	2	1
Thysanoptera	12	1
Zygentoma	0	1
Total	357	112
Total (%)	76	24

Means of introduction (intentional or unintentional)

The vast majority of non-native insects are shown to have been accidentally introduced to the country (89% – 415 species). Intentional introduction occurred at a percentage of only 12%, concerning the deliberate translocation of species for biological control, mainly Hymenoptera (47 species), followed by Coleoptera (6 species) and only one species of Hemiptera.

Regime

The analysed data suggest that one in two of the presented non-native insects are phytophagous (50%), followed by parasitic/predacious taxa (28%) and detritivorous insects (21%) (Table 4).

Discussion

Taxonomy and species richness

Contrary to Avtzis et al. (2017), where Hemiptera dominated other orders in species richness, new additions render Coleoptera as the order holding the highest number of non-native insect species (Fig. 1). Order representation coincides with Roques (2010), as Coleoptera, Hemiptera and Hymenoptera (in descending order) contribute the highest numbers of non-native insects to Europe, as well as to Greece. These orders account for nearly 80% of total non-native insect species in Greece. From a further analysis of some of the most species-rich families within these orders, some general trends can be deducted.

The majority of non-native hymenopteran species (60%) belongs to the superfamily Chalcidoidea that includes some of the most commonly used agents of biological control that are intentionally released, for example, *Coccophagoides utilis* Doutt, 1966 (Argyriou and Kourmadas 1979), *Metaphycus lounsburyi* (Howard, 1898) (Macropodi 1985) and *Semielacher petiolata* (Girault, 1915) (Michelakis and Vacante 1997).

In relation to Hemiptera, the superfamily Coccoidea holds almost half of the non-native true bugs (41%), followed by the family Aphididae (34%). Both taxa include small, phytophagous insects transported through international commerce of infested

Table 4. Regime of non-native insect orders of Greece.

Order	Regime			
	phytophagous	detritivorous	parasitic/predator	unknown
Blattodea	0	3	0	0
Coleoptera	58	69	26	2
Dermaptera	0	2	2	0
Diptera	11	7	6	0
Hemiptera	134	0	6	0
Hymenoptera	10	0	81	0
Lepidoptera	19	8	0	0
Mantodea	0	0	2	0
Phthiraptera	0	0	7	0
Psocoptera	0	13	0	1
Siphonaptera	0	0	3	0
Thysanoptera	12	0	1	0
Zygentoma	0	1	0	0
Total	244	103	134	3
Total (%)	50	21	28	1

plant material (Rabitsch 2010), that are frequently responsible for extensive damage in crops and agricultural plants, for example, *Aphis illinoisensis* Shimer, 1866 (Aggelakis et al. 2005) and *Parasaissetia nigra* (Nietner, 1861) (Tsagkarakis et al. 2016).

Finally, regarding Coleoptera, their numbers extend to a great variety of families; yet, Chrysomelidae, Dermestidae and Nitidulidae seem to hold the largest number of species accounting for almost one third (30.8%) of non-native beetles. These families include some notorious pests that feed on sap, debris, plant material and stored products. For example, non-native species of the genera *Carpophilus* and *Epuraea* (Nitidulidae) have been proven to be major pests of dry, rotten and ripe fruits (Jelínek et al. 2016). Carpet beetles (Dermestidae), such as *Anthrenus coloratus* Reitter, 1881 and *Reesa vespulae* (Milliron, 1939), have been associated with the degradation of leather, animal and wool products, as well as the destruction of museum collections, negatively affecting the preservation of historical cultural heritage (Kovalenko 2018; Tsvetanov and Háva 2020). Additionally, many alien seed-beetles (Chrysomelidae: Bruchinae) have been recorded as pests of a vast spectrum of indigenous and exotic plants (Yus-Ramos et al. 2014). On the contrary, families with wood-boring and saproxylic species (e.g. Cerambycidae, Buprestidae) or ground-dwelling species (e.g. Carabidae) are significantly less represented.

Since the previous study, non-native representatives of three additional insect orders have been recorded in Greece, namely Dermaptera, Mantodea and Zygentoma. The cryptogenic silverfish *Ctenolepisma longicaudata* Escherich, 1905 has been known as a household pest commonly found in attics, cupboards and drawers, first being reported in the country by Mendes (1980). Mantodea are represented in Greece by two alien species, the recently reported giant African mantis *Sphodromantis viridis* Forsskål, 1775 and the giant Asian mantis *Hierodula tenuidentata* Saussure, 1869 (Romanowski et al. 2019; Battiston et al. 2020). Although mantids are considered highly predacious, the ecological impacts of these species on native biodiversity have yet to be studied. Concerning earwigs (order Dermaptera), two species have recently been found in the country, namely *Euborellia femoralis* (Dohrn, 1863), an alien species collected in mainland Greece and the island of Rhodes (Kalaentzis et al., in press) and *Forficula lucasi* Dohrn, 1865, a cryptogenic species collected from the island of Lesvos (Zafeiriou et al. 2021).

Origin – status

In terms of geographic origin, the largest proportion (41%) of alien insect species originates from Asia (i.e. Eastern Palearctic and Indomalaya). This may arise from the increased import of goods from Asian countries (e.g. China, India and Iraq). A recent example of an Asian invader has been the alarming case of *Xylotrechus chinensis* (Chevrolat, 1852). The species was first intercepted from the island of Crete in 2017, causing the increased mortality of several mulberry trees (Leivadara et al. 2018). No more than two years after its initial record, *X. chinensis* had spread to the capital city of Athens, initiating an eradication effort that has resulted, until now, in the trimming and logging of approximately 1300 infested trees. A somewhat smaller, but equally important percentage of alien insect species, originates from the New World (Nearctic and Neotropics; 31%). The Nearctic zoogeographical realm seems to be the primary source of

non-native Hemiptera, Hymenoptera and Diptera, while Indomalaya contributes to the majority of alien Coleoptera and Lepidoptera.

For many non-native insects, it is generally unknown whether their introduction to Greece is the result of a primary introduction event from their area of origin or a secondary translocation from an already invaded country (e.g. Italy or Germany, two of the largest trading partners of Greece). Hosting a record number of 923 non-native insects (Inghilesi et al. 2013), Italy has been previously identified as the most common origin of alien species for Greece (Avtzis et al. 2017). These statistics may highlight the need for stronger customs control on products imported, not only from Asia and America, but also within Europe. However, it is crucial to take into consideration the cryptogenic nature of a high number of non-native species. As 24% of the presented taxa (112 species) are of unknown origin, perhaps even native to the country, the presented results regarding the origin of species should be viewed with healthy scepticism.

The enigmatic origin of cryptogenic species has been viewed as an impediment to the study of biological invasions, possibly obscuring the true impacts, dispersal corridors, success rate, susceptibility or resistance of communities to invasions and management of non-native taxa (Carlton 1996; Jarić et al. 2019). Our results show that almost a quarter of the catalogued species are cryptogenic (Table 3). Information on the true origin of these species might have altered the overall result, such as the main geographical origin of alien insects in the country.

Intentional or unintentional introduction

Deliberate introductions of insects in Greece reflect on releases for the biological control of crop pests. More than half of intentionally introduced species are Hymenoptera, mostly parasitoid wasps of the Chalcidoidea superfamily. Introduced Hymenoptera have long been used in Greece for the biological control of aphids (Aphididae), whiteflies (Aleyrodidae) and scales (Coccoidea) (Paraskakis et al. 1980; Kavallieratos et al. 2001; Japoshvili et al. 2010), pests which are responsible for economic losses in agriculture (i.e. through reduced performance of plants, reduced harvest and succession of secondary fungal or viral infections; Perdikis et al. 2008). Furthermore, aphids and scales have been the target of biological control using lady bugs (Coccinellidae), including, but not restricted to, the Australian ladybugs *Cryptolaemus montrouzieri* Mulsant, 1850 and *Rodolia cardinalis* (Mulsant, 1850) (Roy and Migeon 2010). This family contains all six, deliberately introduced alien beetle species in Greece.

Considering Hemiptera, *Perillus bioculatus* (Fabricius, 1775) has been the only deliberately imported, alien true bug species in the country. During the 1950s and 60s, the species was imported to various European countries (including Greece) for the biological control of the Colorado potato beetle *Leptinotarsa decemlineata* Say, 1824 (Mentzelos 1967; Jermy 1980). Although the species failed to establish at the time, since the beginning of the 21st century, it started re-appearing in Bulgaria, Greece, Moldova and Serbia (Péricart 2010; Protić and Živić 2012; Valeriu and Elisoveţcaia 2014). Whether the presence of *P. bioculatus* in Europe is a result of subsequent accidental introduction events or a previously unnoticed, successful introduction is yet to be clarified.

Regime

Within the broad feeding guilds, certain orders seem to prevail. Specifically, Hemiptera constitute more than 50% of phytophagous insects. This may highlight the infliction of serious damage to the native Greek flora, as recorded for the majority of economically important taxa. However, regarding native plant species, these impacts have been largely unnoticed. For example, as the oak lace bug *Corythucha arcuata* (Say, 1832) was expanding rapidly in the last 20 years all over Europe (Csóka et al. 2020), the long-term impact of this expansion remained unknown and even partly underestimated. However, recent studies have shown that chronic infestations can have a negative impact on the growth and fecundity of oak stands (Franjević et al. 2018; Paulin et al. 2020). Coupled with the general oak decline syndrome that is observed in Europe (Gallego et al. 1999; Mitchell et al. 2019), the impact of *C. arcuata* on oak stands is expected to become even more severe.

Moreover, Hymenoptera seem to dominate parasitic-predacious insects, while Coleoptera contribute to the majority of detritivorous species (Table 4). Considering that the largest percentage of alien terrestrial arthropods are introduced to Europe through the horticultural/ornamental pathway (Rabitsch 2010), the presence of primarily phytophagous non-native insects in the country underlines the necessity of stricter phytosanitary measures in border and customs control, as well as compliance with the International Standards for Phytosanitary Measures (ISPMs), adopted by the Commission on Phytosanitary Measures (CPM).

Conclusions

Though the increase in the number of species non-native to Greece by approximately 80% since their first report (Avtzis et al. 2017) can well be attributed to both previously omitted and new records, it is apparent that invasive insects are steadily becoming a major threat to tackle, both at national and international level. Greece, in particular, situated at the crossroads between Asia, Europe and Africa, is likely to experience pressure from various origins, as demonstrated in the current study. In anticipation of the rise in emerging alien species, the establishment of an efficient early warning system seems to be the only plausible approach, particularly if this is integrated in the current phytosanitary surveys. Only by doing this, supplemented with a frequent and exhaustive update of the checklist of the non-native entomofauna of Greece, is it likely to mitigate the impact of these species in the years to come.

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Author's contribution

Conceptualisation (J.D, K.K, C.K, E.K), Methodology (J.D, D.N.A), Software (J.D, K.K, C.K), Formal analysis (J.D), Investigation (J.D, K.K, C.K, E.K, C.G, D.N.A), Resources, Data Curation (J.D, C.K., K.K.), Writing – Original draft (J.D), Writing – Review and Editing (J.D, K.K, C.K, E.K, C.G, D.N.A), Visualisation (J.D, K.K, C.K, E.K, C.G, D.N.A), Supervision (C.G, D.N.A), Project Administration (C.G, D.N.A), Funding Acquisition (C.G).

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Supplementary material 1

Comprehensive catalogue of the non-native insect fauna of Greece

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Data type: species data

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